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Effects of oligotrophication on primary production in peri-alpine lakes

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[1] During the second half of the 20th century untreated sewage released from housing and industry into natural waters led to a degradation of many freshwater lakes and reservoirs worldwide. In order to mitigate eutrophication, wastewater treatment plants, including Fe-induced phosphorus precipitation, were implemented throughout the industrialized world, leading to reoligotrophication in many freshwater lakes. To understand and assess the effects of reoligotrophication on primary productivity, we analyzed 28 years of ^{14}C assimilation rates, as well as other biotic and abiotic parameters, such as global radiation, nutrient concentrations and plankton densities in peri-alpine Lake Lucerne, Switzerland. Using a simple productivity-light relationship, we estimated continuous primary production and discussed the relation between productivity and observed limnological parameters. Furthermore, we assessed the uncertainty of our modeling approach based on monthly ^{14}C assimilation measurements using Monte Carlo simulations. Results confirm that monthly sampling of productivity is sufficient for identifying long-term trends in productivity and that conservation management has successfully improved water quality during the past three decades via reducing nutrients and primary production in the lake. However, even though nutrient concentrations have remained constant in recent years, annual primary production varies significantly from year to year. Despite the fact that nutrient concentrations have decreased by more than an order of magnitude, primary production has decreased only slightly. These results suggest that primary production correlates well to nutrients availability but meteorological conditions lead to interannual variability regardless of the trophic status of the lake. Accordingly, in oligotrophic freshwaters meteorological forcing may reduce productivity impacting on the entire food chain of the ecosystem.

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1. Introduction

[2] Water pollution affects ecosystems of natural inland waters and leads to the degradation of freshwater rivers, lakes, and reservoirs. In particular, untreated sewage released from housing, industry, and fertilizer-based agricultural practices can result in an oversupply of nutrients to downstream lacustrine systems. Since the mid-20th century, the pollution of lakes and reservoirs with excessive nutrients loads have been recognized as a major threat to freshwater ecosystems [*Vollenweider*, 1968]. Phosphorus (P) and nitrogen (N) loading specifically have been identified as a primary cause of eutrophication of the inland waters [*Dillon and Rigler*, 1974; *Vallentyne*, 1973]. Consequently, sewage treatment plants were constructed to reduce nutrient loading from wastewater and a ban on P-containing detergents was implemented in many industrialized countries [*Barbieri and Simona*, 2001; *Duenas et al*., 2003]. As a direct consequence of these water pollution control measures, nutrients loading declined and water quality in freshwater systems was improved [*Anderson et al*., 2005; *Jeppesen et al*., 2005]. In many systems, a reduction of algal biomass, resulting in an unintended decline of freshwater fishing yields, was observed simultaneously to the oligotrophication process [*Ashley et al*., 1997; *Finger et al*., 2007a; *Stockner et al*., 2000]. This has led fisheries to call for an enhanced phosphate supply to lakes by (1) downscaling the phosphate elimination in sewage treatment plants and (2) artificial fertilization of oligotrophic lakes [*Ashley et al*., 1997; *Finger*, 2006; *Mazumder and Edmundson*, 2002].

[3] The key element connecting fishing yield and nutrients in a freshwater ecosystem is algae growth, quantified by primary productivity. Primary production is a vital link in the carbon (C) cycle between organic and inorganic matter in aquatic systems. Primary productivity can be directly determined by measuring the rate of ^{14}C

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assimilation by living primary producers as described by *Steemann Nielsen* [1952]. The instant C assimilation rate per water volume P^B (mgC m^{-3} h^{-1}) in a freshwater system depends on numerous biotic and abiotic factors including nutrient availability, water temperature, algal biomass, internal mixing processes and light availability.

[4] While many factors change gradually, light intensity fluctuates instantly due to changing solar irradiance and needs to be considered continuously. The relation between in situ light intensity (photosynthetically active radiation; PAR) and P^B has been investigated in the late 1970s [*Jassby and Platt*, 1976; *Platt et al*., 1980]. The mathematical formulation of light-dependent production provides the basis for modeling the primary production of a water body as a function of light intensity [*Behrenfeld and Falkowski*, 1997]. *Finger et al*. [2007b] demonstrated that primary production can be estimated continuously by using the mathematical equation proposed by *Platt and Jassby* [1976] which is based on a high-resolution assessment of surface radiation and linear interpolation of periodically sampled biotic and abiotic parameters. This approach allows estimating continuous primary production in a water body and, hence, is suitable to investigate the temporal development of productivity in freshwaters relying on intervallic sampling of ^{14}C assimilation as well as biotic and abiotic parameters.

[5] In this study, we will investigate the effects of oligotrophication on in situ primary productivity of a peri-alpine lake. In order to understand how areal primary production is reduced by lower nutrient concentrations, we will assess the long-term temporal development of the production irradiance relation (P-I relation) proposed by *Platt and Jassby* [1976]. An understanding of impacts of oligotrophication on the P-I relation is essential to adapt adequate phosphorus elimination measures in tributaries to preserve lake internal productivity at a natural level.

[6] We choose Lake Lucerne for our study, as 28 years of ^{14}C assimilation data are available, as well as other biotic and abiotic parameters such as global radiation, nutrient concentrations and plankton densities. This valuable dataset makes the case study suitable for primary production modeling according to *Finger et al*. [2007b], as described in the method section. Using a simple P-I relation, we will estimate continuous primary production and discuss the linkage of the temporal development of production with other observed parameters. The study concludes by discussing the influence of biotic and abiotic factors on primary production.

2. Study Site

2.1. Geographic Setting

[7] Lake Lucerne is located in central Switzerland at an elevation of 434 m asl. With a volume of 11.8 km^3, a surface area of 114 km^2 and a maximum depth of 214 m it is the fourth largest lake in the country. The 2124 km^2 large catchment is heterogeneous ranging from intensive farmland near the Lucerne area to high alpine headwaters reaching altitudes up to 3630 m asl. The lake is fed by four major inflows, Reuss, Sarner Aa, Engelberger Aa and Muota, and discharges about 3.3 km^3 a^{-1} into the Reuss at the outlet in Lucerne (Figure 1). Accordingly, the mean water residence time in the lake is 3.4 years.

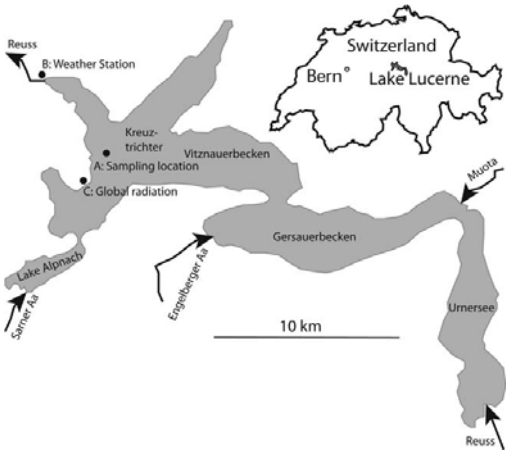

Figure 1. Map of the study site, including sampling sites, (filled circles) on and around Lake Lucerne.

[8] The morphology of the lake is characterized by five basins, (i) Lake Alpnach, (ii) Kreuztrichter, (iii) Vitznauerbecken, (iv) Gersauerbecken, and (v) Urnersee. Ionically heavier water from the Muota River and Lake Alpnach dominate the water column of Kreuztrichter and the surrounding bays, while Urnersee is characterized by soft glacier water from River Reuss [*Schlatter et al*., 1997]. This circumstance leads to a gradual density current in the hypolimnion of the lake from Lucerne to Altdorf and a surface circulation back to Lucerne at the surface of the lake [*Aeschbach-Hertig et al*., 1996]. Accordingly, the subbasin Vitznauerbecken reacts slower to allochthonous nutrient inputs than the subbasin Urnersee. Nevertheless, all our investigations focus on the sampling station Kreuztrichter (Figure 1; location A), as the responsible Governmental Agency considered it to be a representative sampling site, where the central throughput of lake water from all basins is located. ^{14}C assimilation profiling in 1989 at five different sampling sites confirmed the representativeness for phytoplankton primary production of location A (personal communication, P. Bossard).

2.2. Limnological—Ecological Development of the Lake

[9] Lake Lucerne was one of the first Swiss lakes where limnological parameters were monitored in order to investigate the long-term development of the lake ecology [*Bührer and Ambühl*, 2001; *Bürgi and Stadelmann*, 2002]. While nutrient levels in Lake Lucerne (Kreuztrichter) were continuously increasing between 1962 and the end of the 1970s, sewage treatment plants, a ban of phosphate in detergents and water pollution control measures have led to a continuous decline of soluble reactive phosphorus (SRP) in the lake since the early 1980s. Nevertheless nitrate concentrations continue to increase up to the present date.

[10] Obviously, these limnological changes had a direct impact on the phytoplankton diversity in the lake. In the early 20th century, Lake Lucerne was dominated by diatoms, mainly by Cyclotella [*Bachmann*, 1923]. During the eutrophication (from 1950 to 1970) the biomass was

Table 1. Overview of Sampling Program From 1979 to 2007

Parameters	Symbol	Unit	Location[a]	Sampling Period	Sampling Frequency
^{14}C Assimilation[b]	P^B	mgC m^{-3} h^{-1}	A	1979–1997 and 2007	Monthly
Chlorophyll a[b]	*Chla*	mg m^{-3}	A	1979–1997 and 2007	Monthly
In situ PAR	$I_{in\ situ}$	mE m^{-2} s^{-1}	A	1979–1997 and 2007	Monthly
Surface PAR	$I_{surface}$	mE m^{-2} s^{-1}	A	1979–1997 and 2007	Monthly
Global radiation[c]	$I_S^{MeteoSwiss}$	W m^{-2}	B	1981–2007	Hourly
Global radiation	I_S^{Eawag}	mE m^{-2} s^{-1}	C	1983–1997	Hourly
Temperature	T	°C	A	1979–1997 and 2007	Monthly
Secchi depth[d]	s_d	m	A	1979–1997 and 2007	varying
Nitrogen	N	mgN m^{-3}	A	1961–2009	~Monthly
Soluble reactive phosphorus	*SRP*	mgP m^{-3}	A	1955–2010	~Monthly

[a]Locations marked in Figure 1.
[b]Chlorophyll a, temperature and ^{14}C assimilations were determined at the following depths (m): 0, 0.5, 1, 1.5, 2.5, 3.75, 5, 7.5, 10, 12.5, 15, 20, 25, and 30 (note: before 1988 samples at 0.5, 1.5, 3.75, and 12.5 m were interpolated and before 1983 samples at 1 m depth were also interpolated).
[c]Data from MeteoSwiss.
[d]Various sources.

dominated by netplankton and increased from ~20 to ~30 gFW m^{-2}. This development was also reflected by Secchi depth readings (measured during the summer months from April to October), which decreased until the late 1970s. With increasing P-load green algae and chrysophytes became more abundant. While the pennate diatoms remained dominant, the blue-greens almost disappeared toward the end of the eutrophication period.

[11] The ensuing reoligotrophication phase after the late 1970s was characterized by a hysteresis in species composition [*Bürgi*, 1987; *Bürgi and Stadelmann*, 2002; *Bürgi et al*., 1986]. These shifts cannot be explained by bottom-up-control of the phosphorus regime alone [*Bürgi et al*., 1999] and it is assumed that such species shifts are of long-term character and not immediately reversible. Phytoplankton biomass unexpectedly fluctuated between ~20 (in 1980s) and ~40 gFW m^{-2} (1996), before it dropped most recently to less than ~15 g FW m^{-2}. The euphotic zone (> 1% of PAR surface radiation) slightly increased from 15 (1979) to 19 m (1993), while Secchi depth readings (summer averages) increased from 4 (1980) to 5.5 m (1995). During this period nanoplankton (predominantly small flagellates) became the dominant species. This change in the phytoplankton composition has very likely lead to a shift of the Redfield-ratio (P:N:C) within the phytoplankton community (toward less P per N and C), driven by the continuous decrease of phosphorus concentrations [*Bührer and Ambühl*, 2001]. Today, the functional properties of Lake Lucerne are similar to the former oligotrophic conditions ~50 years ago. The lake shows functional but not structural resilience: today's oligotrophic community structure differs from the original one of the early 1960s.

[12] While these long-term observations have been documented in various publications [*Bossard and Ambühl*, 1984; *Bossard and Bürgi*, 2007; *Bührer and Ambühl*, 2001; *Bürgi and Stadelmann*, 2002], the long-term ^{14}C assimilation rates have never been analyzed. However, the biotic and abiotic parameters described above have a direct effect on primary production. The effects of oligotrophication on productivity is expected to be complex as lower P-concentrations can be compensated by higher C:P ratios [*Hessen et al*., 2002] and lower biomass increases the euphotic depth [*Jaun et al*., 2007]. Accordingly, an assessment of the effects of lower nutrients on primary production is essential in order to understand observed changes in the phytoplankton community and identify potential processes leading to declining fishing yields.

[13] In the present study we present long-term C assimilation rates of phytoplankton, P^B, in the lake collected between 1979 and 1997 and during 2007. By modeling continuous production and investigating the development of the key model parameters, we intend to give a thorough description of the oligotrophication history of Lake Lucerne, assessing essential fundamentals for investigations on plankton compositions shifts. The study concludes by assessing the sensitivity of productivity to oligotrophication, meteorological conditions, and other external factors.

3. Material and Methods

[14] In this study we assess temperature, nutrients, chlorophyll a, light intensity and primary production rates collected in the framework of the lake monitoring for the years 1979–1997 as well as 2007 and we present a modeling approach which allows determining sensitivity of primary production to environmental factors. An overview of all data presented in this study is given in Table 1.

3.1. Existing Data From Long-Term Monitoring

[15] Profiles of primary productivity in Kreuztrichter (Location A, Figure 1) were measured between January 1979 and November 1997 and in 2007. Altogether, 265 vertical profiles were collected, resulting in an average of one sample set every 25 days. Primary production was measured by determining in situ ^{14}C assimilation in 0, 0.5, 1, 1.5, 2.5, 3.75, 5, 7.5, 10, 12.5, 15, 20, 25, and 30 m depths. Before 1987, some depth steps were interpolated. C assimilation was determined with the ^{14}C technique [*Nielsen*, 1980] modified according to *Gächter and Mares* [1979] by using the acid bubbling method. As described in *Bossard et al*. [2001], two 120 mL samples were inoculated with 5 □Ci NaH$^{14}CO_3$ in Duran bottles (one opaque sample and one with transmission properties of 22% adsorption at 235 nm and 4% at 350 nm). Both bottles were incubated in their corresponding depths for approximately 4 h between 10 and 14 h local time (central European time). Hence, the amount of ^{14}C assimilated by the algae multiplied by the total dissolved inorganic carbon (DIC) in the incubated

water sample corresponds to the instantaneous P^B. DIC was calculated from alkalinity [*American Public Health Association*, 1971]] and *pH* following *Rodhe* [1958] and *Golterman et al*. [1978]. Furthermore, all P^B values were corrected for nonphotosynthetic fixation of C by subtracting P^B determined in the dark sample. Details of the acid bubbling method and incubation methods have been described by *Gächter et al*. [1984] and *Sakamoto et al*. [1984].

[16] Between 3 January 1979 and 17 November 1997 chlorophyll *a* concentrations (*Chla*, mg m^{-3}) have been assessed on a monthly basis in subsamples of P^B-water samples. *Chla* was determined according to *Deutschen Einheitsverfahren* (*DEV*) [1972–1989]. Water samples were filtered through Whatman GF/F filters, and placed into Sovirel tubes filled with 8 mL of 90% ethanol. Subsequently, *Chla* was extracted from the samples in a water bath at 75°C and sonification. After a further filtration through Millipore Millex FG 0.2 □m membrane filters, *Chla* content was determined spectrophotometrically following *DEV* [1972–1989] using a U2000 dual path spectrophotometer (Hitachi, Japan). Simultaneous to sampling water temperature was measured with a WTW probe (Conductivity-meter LF 191, Weinheim, Germany) at the same depths. Further details on chemical analysis of water samples are explained in *Bossard et al*. [2001].

[17] SRP and total P were determined photometrically using the ammonium molybdate method [*DEV*, 1972–1989] according to *Ambühl and Schmid* [1965]. They were measured on a monthly basis in 0, 2.5, 5, 7.5, 10, 12.5, 15, 17.5, 20, 30, 50, 75, 100, and 110 m depth.

[18] Vertical profiles of in situ photosynthetically available radiation $I_{in\ situ}$ (□E m^{-2} s^{-1}) was measured at location A with a scalar quantum sensor (LI 190 SB) connected to an integrating LI 188 quantum meter (LI-COR Inc., USA). A second sensor placed at the lake surface (location A, Figure 1) served as a simultaneous reference measurement. The light profiles have been collected simultaneously to water sampling, which is important in order to determine the relation between P^B and $I_{in\ situ}$ as outlined below.

[19] Surface solar radiation $I_S^{MeteoSwiss}$ (W m^{-2}) is continuously recorded by the Federal Office of Meteorology and Climatology (MeteoSwiss) since 1981 close to the City of Lucerne (location B, Figure 1). Additionally, photosynthetic active radiation, I_S^{Eawag} (□E m^{-2} s^{-1}), was measured on top of the Eawag laboratory building (location C; Figure 1), at only 5 km from the sampling site (location A; Figure 1) between 1983 and 1997. As MeteoSwiss started its monitoring in 1981, the recordings from the Eawag building were used for modeling purposes prior to 1981.

3.2. Primary Production Model

[20] In order to model continuous primary production in the lake, we rely on a method similar to *Finger et al*. [2007b] which allows to estimate P^B for any given time using continuous global radiation measurements and the experimental data described above. In the following we outline the mathematical modeling approach.

[21] *Chla*-normalized C assimilation rate $P^{Chla} = P^B/Chla$ (mgC h^{-1} (mg*Chla*)$^{-1}$), was determined for all P^B-samples. Subsequently, all P^{Chla} were normalized from measured in situ temperature (T) to a reference temperature ($T_{norm} = 10$°C), assuming exponential T-dependent growth rates:

$$P_{norm}^{Chla}(z) = P^{Chla} \cdot e^{(\ln(Q_{10})(T_{norm}-T)\div 10)} \quad (1)$$

[22] As previous studies demonstrated that Q_{10} varies between 1.88 and 2.5 [*Eppley*, 1972; *Eppley and Sloan*, 1966; *Williams and Murdoch*, 1966] we fixed $Q_{10} = 2$, denoting the logarithmic growth increase for 10°C warming. The normalized C assimilation rates $P_{norm}^{Chla}(z)$ is primarily a function dependent on ambient light intensity ($I_{in\,situ}$). Accordingly, $P_{norm}^{Chla}(z)$ is directly dependent on $I_{in\ situ}$ [*Platt et al*., 1980]:

$$P_{norm}^{Chla}(z) = P_S^B \left(1 - e^{-\frac{\alpha I_{in\,situ}}{P_S^B}}\right) \cdot e^{-\frac{\beta I_{in\,situ}}{P_S^B}} \quad (2)$$

where P_S^B stands for the hypothetical maximal photosynthetic C assimilation without photoinhibition, and □ denotes the increase of $P_{norm}^{Chla}(z)$ with increasing $I_{in\ situ}$ (z) and □ stands for the decrease of $P_{norm}^{Chla}(z)$ caused by photoinhibition. All three parameters were determined for every available profile of $P_{norm}^{Chla}(z)$ by minimizing the sum of the square errors. Fitted parameters were crosschecked for plausibility for each profile, making sure that photoinhibition term cannot become negative. The sum of the square errors remained for most profiles below 10% of the total sum, revealing adequate curve fitting similar to that presented by *Finger et al*. [2007b].

[23] Likewise to *Finger et al*. [2007b] we linearly interpolated □, □, water T and the light attenuation based on the PAR profiles. The relative light I_{rel} (z) is determined by the quotient of $I_{in\ situ}$ (z) and $I_{surface}$ (t). Assuming that water turbidity is not subject to short-term fluctuations, the I_{rel} (z)profiles were interpolated linearly between sampling days. Finally, $I_{in\ situ}(z,t)$ can be computed for every modeling time step by multiplying I_{rel} (z,t) with $I_{surface}$.

[24] The highly resolved series of $I_{surface}$ (t) were determined by scaling the high resolution recordings of MeteoSwiss ($I_S^{MeteoSwiss}(t)$) to values recorded at the sampling site A during sampling. The linear scaling factor $c = 2.143$ □E s^{-1} W^{-1} accounts for unit conversion (W m^{-2} to □E m^{-2} s^{-1}) and for mean differences in sun light exposure at the two locations. For the period prior to 1981 the continuous surface recording at the Eawag building (location C; Figure 1) were linearly scaled to the sampling location A.

[25] Based on the determined high resolution surface radiation $I_{surface}$ (t), $P_{norm}^{Chla}(z)$ can be estimated for any given $I_{surface}$ (t), assuming that the parameters of equation (2) can be interpolated linearly between two samplings. Subsequently, $P_{norm}^{Chla}(z)$ was back transformed from T_{norm} to ambient T using the inverse of equation (1):

$$P^{Chla}(z;t) = P_{norm}^{Chla}(z;t) \cdot e^{(\ln(Q_{10})(T(z;t)-T_{norm})\div 10)} \quad (3)$$

[26] Finally, P^{Chla} (z,t) has to be multiplied with the lineally interpolated *Chla* (z,t) in order to obtain the actual P^B (z,t). With this approach P^B-profiles can be obtained for every recording of $I_S^{MeteoSwiss}$ and by integrating P^B (z) over the entire photic layer areal productivity can be obtained for every time step.

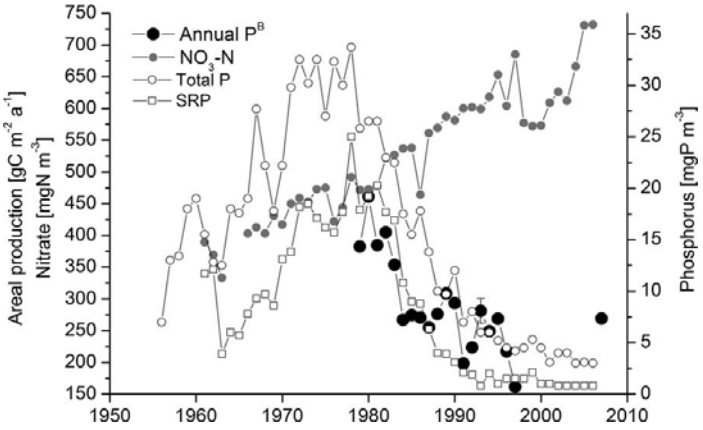

Figure 2. Long-term development of nutrients concentrations and annual productivity in Lake Lucerne. The legend in the top left corner describes the symbols.

3.3. Uncertainty Assessment of Modeling

[27] The linear interpolation of the parameters in equation (2) engenders uncertainty, as all factors may not change linearly between two samplings. However, linear interpolation appears to be the most plausible way to estimate continuous primary production in the lake with the available datasets. In order to estimate the uncertainty due to the monthly sampling, we used a Monte Carlo (MC) simulation approach which consists of a random selection subsamples from a pool of available sampling profiles as explained in the following.

[28] In 1993, the monitoring campaign was exceptionally intensified and 24 samplings were conducted instead of the usual monthly profiles. By selecting randomly 12 profiles out of the 24 available profiles the uncertainty generated by the selection of 12 sampling dates can be assessed. This is a measure for the uncertainty assuming that biweekly measurements cover full variability of the modeling approach as outlined in the discussion section. For this purpose, we selected 100 times 12 profiles from the 24 profiles available and computed the annual areal production as described in section 3.2. Hence, the range of the 100 runs with 12 randomly selected profiles represents the uncertainty produced by a monthly sampling frequency.

[29] Furthermore, we assessed the dependency of uncertainty of our modeling approach on the number of profiles available by varying the number of profiles selected randomly from the 24 profiles. This allows us to discuss the number of profiles necessary in order to maximize the ratio between uncertainty and fieldwork load. For this purpose, we performed the MC simulations described above by changing the number of profiles selected from the 24 available profiles.

4. Results

4.1. Long-Term Development of Limnological Parameters

[30] As expected the most evident factor influencing productivity in Lake Lucerne is the bioavailable phosphorus in the lake, which has gone through a massive input alteration by anthropogenic activities in the catchment since the mid-1950s. In Figure 2, the development of total phosphorus, SRP and NO_3-N is compared to annual primary productivity. The development of total phosphorus in the lake distinctly illustrates eutrophication until the late 1970s with total phosphorus concentrations rising to above 30 mg m^{-3}. Reoligotrophication started in the early 1980s leading to a continuous decline of phosphorus to below 5 mg m^{-3} in recent years. Between 1979 and 1991, the nutrient levels (disregarding NO_3-N) appear to reflect the annual productivity almost perfectly. While SRP concentrations have continuously dropped from around 20 mg m^{-3} during the late 1970s and early 1980s to below 2 mg m^{-3} in the late 1990s, nitrate concentrations are still continuously rising from around 300 mgN m^{-3} in the 1960s to over 700 mgN m^{-3} in the early 2000s. Annual productivity has continuously been declining since the early 1980s from ~450 to ~270 gC m^{-2} a^{-1} in the early 1990s. It is most probable that this decline is linked to the decline of the production-limiting SRP concentrations. Nevertheless, since 1991 phosphate concentration have remained below ~2 mgP m^{-3} while annual productivity appears to fluctuate between ~150 and ~270 gC m^{-2} a^{-1} (Figure 2). The most recent C assimilation monitoring revealed even an annual productivity of 270 gC m^{-2} a^{-1} in 2007, consistent with the productivity in the 1990s, as the phosphorus concentrations have remained below 5 mgP m^{-3} during the last two decades.

[31] The long-term developments between 1979 and 1997 of radiation, *T* and *Chla*, do not indicate strong trends explaining the decrease in annual productivity presented above (Figure 3 and Table 2). Secchi depth recordings appear to increase to ~12 m during winter time and reach minimum depths of ~3 to 4 m during summer time. Accordingly, the euphotic depth increased up to ~28 m during winter and declined to below ~10 m during summer. Surface water *T* frequently drops below 6°C during winter and reaches more than 20°C during most summers. Accordingly, the volume-weighted water *T* in the

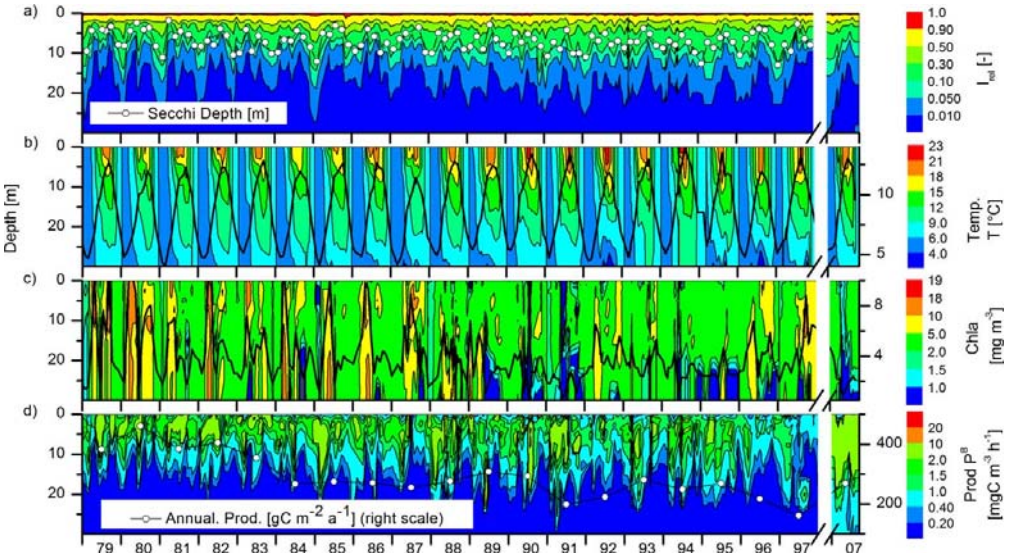

Figure 3. Limnological parameters monitored in Lake Lucerne from 1979 to 1997 and 2007. (a) Relative radiation compared to global radiation at the surface of the lake. The white circles indicate Secchi depth recordings. (b) In situ temperature and volume weighted (black line) water temperature in the top 30 m. (c) In situ and volume weighted (black line) chlorophyll a concentrations. (d) Measured volume specific in situ carbon assimilation rates. The white circles indicate annual areal primary production.

euphotic zone drops to 5°C in winter and rises above 12°C in summer. The *Chla* concentration appears to be very dynamic, reaching frequently concentrations above 5 mg*Chla* m^{-3}, but also dropping below 0.5 mg*Chla* m^{-3}. Since the late 1980s *Chla* concentrations below 20 m depth drop frequently below 0.5 mg*Chla* m^{-3}, while abundance in the surface layer remains above 2 mg*Chla* m^{-3}. The volume-weighted *Chla* concentrations also show a continuous decline over the entire observational time period. Finally, measured C assimilation rates display also a very dynamic pattern. Most of the depth specific C assimilation rates vary between 0 and 2 mgC m^{-3} h^{-1}, except for very few values in the late 1980s reaching 20 mgC m^{-3} h^{-1}. Almost all P^B (z) profiles depict a typical decline of production due to photoinhibition at the surface, a maximum of productivity somewhere in the top 10 m of the water column and a gradual decline in deeper layers due to light limitation, falling in line with observations in other Swiss lakes [*Finger et al.*, 2007b]. The annual primary production computed with this method also indicates a steady decline of productivity since the start of the measurements. Nevertheless, in the beginning of the 1990s productivity appears to steady out between 150 and 270 gC m^{-2} a^{-1}. We will discuss the development of productivity below in more detail.

Table 2. Tendencies of Limnological Parameters Between 1997 and 2007

Parameter	Symbol	Unit[a]	Slope[b]	R^2	p value
Secchi depth	s_d	cm a^{-1}	7.9	0.07	0.0002
Volume weighted temperature	T	°C a^{-1}	0.03	0.01	0.044
Volume weighted chlorophyll a	*Chla*	mg m^{-3} a^{-1}	−0.10	0.09	2.06×10^{-7}
Soluble reactive phosphate	*SRP*	mgP m^{-3} a^{-1}	−0.69	0.71	1×10^{-8}
Annual areal productivity	P^B	gC m^{-2} a^{-2}	−7.4	0.45	7.26×10^{-4}

[a]Unit of the slope of a linear regression through the observed parameter.
[b]All regressions were computed for the period 1979–2007, not accounting for years without data availability.

4.2. Uncertainty of Annual Productivity Estimates

[32] The high fluctuation of annual productivity estimates depicted in Figure 3 call for an assessment of the uncertainty generated by the linear interpolation of the parameterization of the P-I relation. As outlined in the method section above, this was performed with a MC approach, by selecting a subsample of 12 profiles from 24 profiles available for the year 1993. The results indicate that already after 100 MC simulations performed with 12 randomly selected profiles from the year 1993 the annual areal production steadies out at ~275 gC m^{-2} a^{-1}, with a standard deviation from the mean of 6 19 gC m^{-2} a^{-1} (Figure 4a). This result reveals that the common practice of sampling primary production once per month leads to an uncertainty in our annual areal production of 6 7% compared to the intensive sampling in 1993 when productivity was sampled on a biweekly basis.

[33] Furthermore, the fact that after 100 MC-runs the average and the standard deviation of the average appear to become constant allows us to perform an assessment of the uncertainty generated by the number of profiles considered

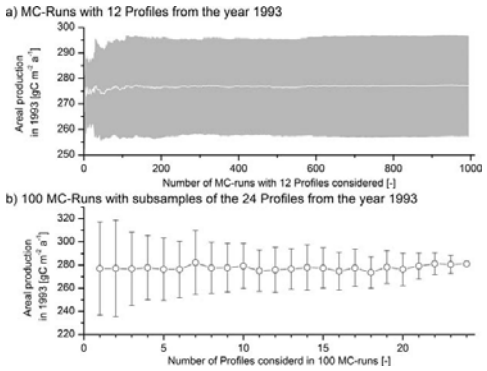

Figure 4. Monte Carlo simulations of annual areal production using a subsample of the 24 profiles measured in 1993. In (a) 1000 MC runs were performed using 12 profiles selected randomly from the entire available data set of 24 profiles and (b) 100 MC runs were performed using different numbers of measured profiles, ranging from 1 to 24 per year.

in the annual production estimation. In Figure 4b, the average and its standard deviation of annual areal production based on 100 MC runs considering a subsample of the available sampling in 1993 are illustrated. If only one profile is randomly chosen to compute areal production the standard deviation amounts up to 15% of the mean production. As expected the standard deviation decreases almost linearly if more sampling profiles are chosen and by definition the standard deviation drops to zero if all profiles are used for the computation. Accordingly the standard deviation can only be considered as an increase of uncertainty in respect to an estimation using all available profiles. In conclusion the uncertainty of our estimations using monthly sampling quantified to be about 6 7%.

4. 3. Aggregation of Productivity

[34] The evolution of primary production in Lake Lucerne, as illustrated in Figure 2, is evident and it seems clear that a reduction of SRP leads to an important reduction of primary production. However, no clear trends can be observed in turbidity, water *T* and *Chla* concentrations (Figure 3 and Table 2). To compare C assimilation rates from different periods of different nutrient levels, the measured C assimilation rates have to be normalized to a reference water temperature and per *Chla* unit. In Figure 5, all available normalized C-profiles have been averaged to monthly means distinguishing between three time periods: (i) mesotrophic phase from 1979 to 1984, (ii) transition phase from 1985 to 1990, (iii) oligotrophic phase from 1991 to 1997, and (iv) the most recent measurements in the year 2007. The aggregated data reveals interesting changes in the primary productivity of the lake. During the mesotrophic phase two distinct seasonal production peaks in spring and fall can be identified with a depression during summer. This is in accordance with two distinct algal peaks observed during this period [*Bossard and Ambühl*, 1984; *Bürgi and Bossard*, 2007]. During the transition phase these peaks become less obvious and frequently only one production maximum can be observed in summer. During the oligotrophic phase in the early 1990s the production peaks are less emphasized than during the eutrophic phase. The characteristics of the seasonal dynamics observed during the early 1990s appear to have become more emphasized during the last sampling year 2007. Indeed, sampling in 2007 revealed two production peaks with production reaching down to 30 m depth and the second peak occurring later in the season. It appears as if under oligotrophic

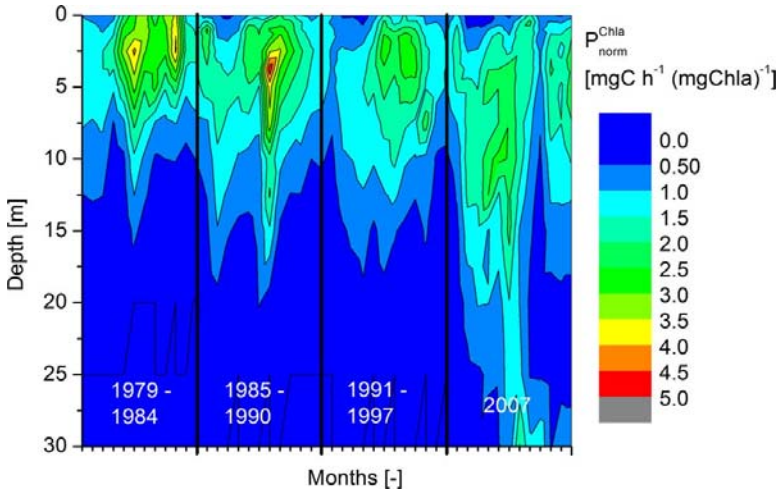

Figure 5. Mean monthly specific C assimilation rates per unit chlorophyll a and normalized to the reference water temperature T_{norm}. Mean monthly profiles have been averaged for the early 1980s (1979–1984), the late 1980s (1985–1990), the 1990s (1991–1997), and 2007.

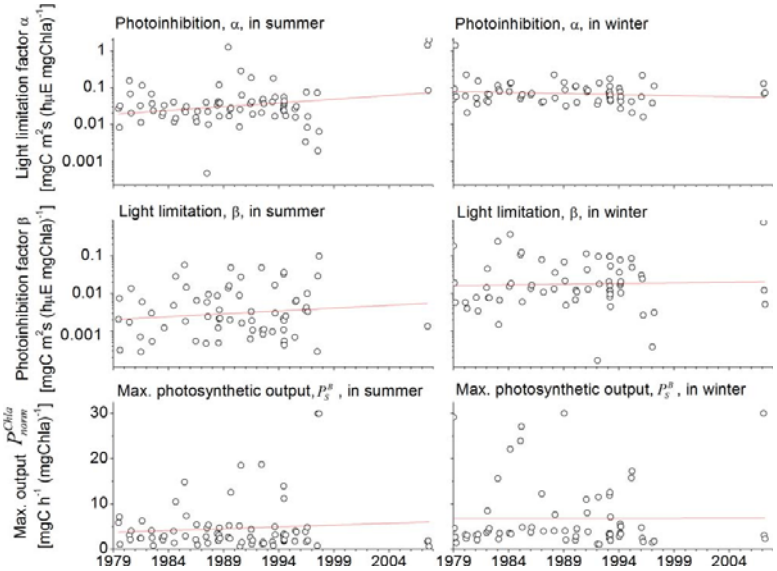

Figure 6. Long-term trends of the three key parameters of the primary production model during (left) summer months (June to August) and (right) winter months (January to March).

conditions C assimilation occurs at a low level everywhere in the lake as soon as light availability is favorable.

4.4. Long-Term Trend in the Irradiance Productivity Relation

[35] The P-I relation described in equation (2) is the fundamental mathematical description of primary production at ambient light availability in aquatic systems. In regard to the drastic decline of productivity from ~450 gC m^{-2} a^{-1} in the 1970s to less than ~270 gC m^{-2} a^{-1} in recent years, it seems logical that there must be a long-term change of the P-I relations over the last three decades. From a mathematical perspective, it is trivial to investigate the long-term trends of the three model parameters of equation (2). In Figure 6, the trends of fitted parameter values for the photoinhibition factor, □, the light limitation factor, □, and maximum photosynthetic output, P_S^B, are illustrated for all summer months (June to August) and winter months (January to March). We intentionally left out spring and fall months, as during these periods production is especially dynamic and long-term trends might strongly be affected by particular sampling days [*Finger et al*., 2007a; *Sommer et al*., 1986].

[36] During summer time the numeric values of all three parameters appear to slightly increase during the 28 year period. This would indicate that production has become more sensitive to photoinhibition, less sensitive to light limitation and maximum output might have increased slightly. However, the coefficients of determination, R^2, are very low (0.0013 for □, 0.043 for □, and −0.0056 for P_S^B), indicating that the observed trend is statistically not significant. Indeed, productivity sampling depends strongly on local weather conditions and accordingly it is difficult to determine significant temporal developments on disaggregated observations (see also discussion above). Similar observation can be made during the winter months. Just as in summer none of the temporal evolutions are statistically significant and the trends are very dependent on individual sampling days.

[37] The lack of clear temporal trends in the key parameters during the entire oligotrophication period indicates that the relation between irradiance and productivity is not directly dominated by the effect of the trophic state of Lake

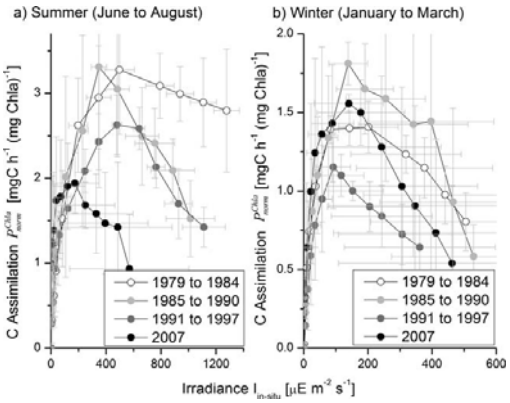

Figure 7. Relation between long-term mean in situ irradiance $I_{in\ situ}$ and mean in situ C assimilation rates $P_{norm}^{Chla}(z)$. Measured averages during the (left) summer months (June to August) and (right) winter months (January to March) are illustrated for 4 time periods during oligotrophication. Error bars indicate standard deviation from the mean.

Lucerne. Moreover, a hysteresis can be observed in the relation between productivity and the decline of the trophic status of the lake. Average profiles, as illustrated in Figure 5, indicate that the productivity indeed changed during the last three decades.

[38] In Figure 7, the P-I relations based on average profiles from four time periods are illustrated in order to show the changes in the P-I relationship during the oligotrophication phase. Again, we restrained ourselves to the summer months (June to August) and winter months (January to March) in order to avoid extreme events during spring and fall which might lead to misinterpretation of long-term trends. As the standard deviations from the means are substantial, the interpretation of the observed changes in the average profiles is only of indicative nature. During the summer months a distinct development of the P-I relation can be observed between the four time periods (section 4.3). During the mesotrophic phase in the early 1980s production P_S^B was above 3 mgC h^{-1} (mg*Chla*)$^{-1}$ even at very high inhibiting irradiance above 1000 □E m^{-2} s^{-1}, dropping to 0 only at very low irradiance below 100 □E m^{-2} s^{-1}. During the transition phase (1985–1990) a drastic decline of productivity at irradiance above 350 □E m^{-2} s^{-1} can be identified. This decline becomes even more distinct as oligotrophication advances. In the 1990s, mean productivity at optimal light condition remains below 2.6 mgC h^{-1} (mg*Chla*)$^{-1}$. The average P-I relation in summer 2007 shows an even more pronounced photoinhibition of productivity at irradiance above 200 □E m^{-2} s^{-1}, with productivity at optimum irradiance below 2 mgC h^{-1} (mg*Chla*)$^{-1}$.

[39] During the cold winter months (January to March) the changes due to oligotrophication is less pronounced than during the warm and sunny summer months. Indeed, average productivity in winter is reduced to a level comparable to the summer months in 2007. During all four trophic levels (section 4.3) the mean productivity at optimal irradiance remains below 1.8 mgC h^{-1} (mg*Chla*)$^{-1}$ and photoinhibition appears to take effect at already 150 □E m^{-2} s^{-1}. Accordingly, it is not possible to distinguish a clear trend during the last three decades of oligotrophication.

5. Discussion

[40] Primary production in aquatic ecosystems is a complex process which can only be partially described with numerical models. The effort to investigate natural processes and interactions of biotic and abiotic parameters in a lake are certainly worthwhile, as they are a valuable tool to quantify and identify key processes leading to observed changes in the ecosystem and to evaluate sensitivities and interdependences.

[41] The 28 year long dataset of primary production would, without aggregation of the raw data, not reveal any significant temporal trends (Figure 3 and Table 2). However, the aggregated data clearly shows that areal productivity decreased simultaneously with the declining phosphorus concentrations (Figure 2). Indeed, only aggregation of the collected data leads to a result which indicates that low nutrients availability has an effect on primary productivity. The estimation of annual areal production based on the P-I relation (equation (2)) reveals, that annual productivity declines almost linearly with declining phosphorus concentrations, at least for mesotrophic levels. During maximal phosphorus pollution in the 1970s productivity is estimated to amount up to ~450 gC m^{-2} a^{-1}. This indicates that production during that time was light-limited due to algal light attenuation. However, since SRP concentrations have dropped below 10 mg m^{-3} variability of annual productivity ranged from 150 to 270 gC m^{-2} a^{-1} during the succeeding 8 years of monitoring. Indeed, this variability falls in line with observations in other oligotrophic lakes [*Goldman*, 1988; *Goldman et al*., 1989; *Jassby et al*., 1990] and can directly have an impact on plankton abundance and fishing yields [*Dubois et al*., 2008; *Rellstab*, 2008; *Rellstab et al*., 2007]. Primary production, being the first element in the food chain, certainly plays a key role in these observations.

[42] Statistical analysis of the long-term data series reveal that significant trends can only be observed in productivity and phosphorus concentrations (Table 2). Furthermore, the MC simulations performed with a subset of the available datasets revealed that the uncertainty of our method is about threefold smaller than the interannual fluctuations or long-term tendencies of productivity. This makes our estimations significant and trustworthy. Furthermore, the MC assessment showed that our method, based on monthly ^{14}C measurements, appears to be an adequate compromise between field effort and uncertainty reductions.

[43] Given the discussed uncertainties, it appears that primary production is indeed subject to large variability. As average P-I profiles from the four trophic phases indicate, it is in particular the photoinhibition term which appears to become more dominant as oligotrophication advances. While in the late 1970s mean production in summer reached 3 mgC h^{-1} (mg*Chla*)$^{-1}$ even at 1000 □E m^{-2} s^{-1}, it has dropped below 1.5 mgC h^{-1} (mg*Chla*)$^{-1}$ in recent years. This suggests that in nutrient-poor environments the biology reacts sensitive to external factors, in this case high radiation, while in eutrophic systems photoinhibition plays a smaller role.

[44] The presented data indicates that the effect of lower nutrients availability on productivity is characterized by a hysteresis. While we could assess the main effects of lower nutrients on productivity further investigations are necessary in order to fully understand the meteorological, biotic and abiotic factors responsible for the variability of the annual areal production in recent years. This complexity of evolving lake ecology requires a long-term monitoring of limnological parameters only available for a few lakes such as Lake Tahoe, California-Nevada [*Goldman*, 1990; *Jassby et al*., 1999], Crater Lake, Oregon [*Larson et al*., 2007] or Mondsee in Austria [*Dokulil*, 1987] to name a few representative examples.

[45] A reduction of plankton abundance in natural waters leads to an increase of the euphotic depth [*Jaun et al*., 2007]. Consequently, the productive water volume increases, partially counter balancing the effect of oligotrophication. Furthermore, plankton composition has to be considered when changes in annual C assimilation are interpreted. Plankton communities adapt to the low-nutrient environment [*Bürgi and Bossard*, 2007], increasing the C:P ratio in phytoplankton [*Van Donk et al*., 2008]. In contrast to algae, C:P ratios in zooplankton remain more constant, as starvation and food enrichment experiments

have shown [*Andersen and Hessen*, 1991]. Accordingly, the total mass of food requirement for zooplankton in oligotrophic waters is higher than in mesotrophic waters. This falls in line with the top-down plankton reduction described in the long-term data description of Lake Lucerne [*Bossard and Ambühl*, 1984; *Bossard and Bürgi*, 2007; *Bührer and Ambühl*, 2001].

[46] The two factors, increasing euphotic depth and changing C:P ratio in phytoplankton, lead to a nonlinear dependence of productivity on nutrients. This is expressed by the long-term development of nutrients availability and productivity: productivity decreased by a factor of 2, while nutrients have decreased by almost 1 order of magnitude. Consequently, primary production in oligotrophic system is not linearly dependent on nutrients availability. This is certainly also a reason for the substantial fluctuation of annual productivity of ∼20% in recent years.

6. Conclusions

[47] The effect of oligotrophication on primary production in Lake Lucerne were quantified for a time period of 28 years (1979–2007) using a numerical modeling approach based on a productivity-irradiation relation first described by *Platt et al* [1980]. The results of the simulations clearly demonstrate the successful reoligotrophication of Lake Lucerne, reducing annual areal primary production from over 400 gC m^{-2} a^{-1} in the late 1970s to less than 270 gC m^{-2} a^{-1} in recent years. For a given trophic status areal annual productivity seems to vary by ∼20% due to external factors such as meteorological variability, falling in line with observations made in other oligotrophic lakes [*Goldman*, 1988; *Goldman et al*., 1989; *Jassby et al*., 1990]. Based on the 28 years of data and the modeling assessment the following conclusions can be drawn:

[48] 1. When the trophic status of Lake Lucerne had reached the maximum phosphorus concentration (> 30 mgP m^{-3} of total P and > 20 mgP m^{-3} of SRP) and nitrate concentrations (> 20 mgN m^{-3}) in the late 1970s, when the annual areal productivity varied between 380 gC m^{-2} a^{-1} and ∼450 gC m^{-2} a^{-1}. Since then water pollution control measures have led to a gradual decrease of phosphorus concentrations in the lake reaching almost natural levels (< 5 mgP m^{-3} of total P and < 2.5 mgP m^{-3} of SRP) by the mid 1990s while nitrate concentrations continued to rise. The annual areal productivity has been continuously decreasing since the 1970s, dropping below 270 gC m^{-2} a^{-1}. This confirms the expectations based on the nutrient molar ratio that productivity in Lake Lucerne was strongly phosphate-limited throughout the observation period.

[49] 2. The presented method of model-based integration of measured monthly C assimilation rates provides significant and reliable annual production estimates. Based on 100 Monte Carlo simulations, with 12 sampling profiles selected randomly from 24 available profiles, measured during an intensive field campaign in 1993 proved that uncertainty of annual productivity estimations based on monthly profiles lies at ∼7%.

[50] 3. Concentrated productivity in the surface layer and shallower Secchi depth recordings than today indicates that during maximal eutrophication in the 1970s C assimilation was light-limited due to light attenuation by algae. In the following decade a reduction of nutrients availability and simultaneous widening of the photic layer was observed. The deepening of the photic layer counter balances substantially the effects of decreasing nutrients availability on productivity, revealing a substantial aspect of the hysteresis of the oligotrophication process.

[51] 4. Individual long-term trends in governing model parameters, such as photoinhibition, light limitation and maximum photosynthetic output, are not significant. Nevertheless, integrated lake system data generated with our modeling approach show a clear development of patterns in limnological parameters, leading finally to the expected decrease of annual areal productivity. Our assessment also shows that during the eutrophic phase typically two productivity maximum occurred at the beginning of summer and at the end of summer. With ongoing oligotrophication three consistent features have been observed: (i) the double-peak productivity maximum becomes less pronounced, (ii) productivity becomes more dynamic, and (iii) productivity reaches to greater depths where algal growth occurs at low irradiance.

[52] 5. Finally, based on our assessments we conclude that meteorological forcing lead to an interannual variability of productivity of ∼20%. In oligotrophic systems this variability may have drastic impacts on the entire food chain of the lake ecosystem.

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References

Aeschbach-Hertig, W., R. Kipfer, M. Hofer, D. M. Imboden, and H. Baur (1996), Density-driven exchange between the basins of Lake Lucerne (Switzerland) traced with the H-3-He-3 method, *Limnol. Oceanogr.*, *41*(4), 707–721.

Ambühl, H., and M. Schmid (1965), Die Bestimmung geringster Mengen von Phosphat-Ion im Wasser von Binnenseen, *Schweiz. Z. Hydrol.*, *27*(1), 184–192.

Andersen, T., and D. O. Hessen (1991), Carbon, nitrogen, and phosphorus-content of fresh-water zooplankton, *Limnol. Oceanogr.*, *36*(4), 807–814.

Anderson, N. J., E. Jeppesen, and M. Sĭndergaard (2005), Ecological effects of reduced nutrient loading (oligotrophication) on lakes: An introduction, *Freshwater Biol.*, *50*(10), 1589–1593.

American Public Health Association (1971), *Standard Methods for the Examination of Water and Wastewater*, New York.

Ashley, K., L. C. Thompson, D. C. Lasenby, L. McEachern, K. E. Smokorowski, and D. Sebastian (1997), Restoration of interior lake ecosystem: The Kootenay Lake fertilization experiment, *Water Qual. Res. J. Can.*, *32*(2), 295–323.

Bachmann, H. (1923), *Charakterisierung der Plaktonvegetation des Vierwaldstättersees mittels Netzfängen und Zentrifugenproben*, Festband H. Christ. Verhandl. Natf. Ges. Basel, Basel, Switzerland.

Barbieri, A., and M. Simona (2001), Trophic evolution of Lake Lugano related to external load reduction: Changes in phosphorus and nitrogen as well as oxygen balance and biological parameters, *Lakes Reservoirs Res. Manage.*, *6*(1), 37–47, doi:10.1046/j.1440-1770.2001.00120.x.

Behrenfeld, M. J., and P. G. Falkowski (1997), A consumer's guide to phytoplankton primary productivity models, *Limnol. Oceanogr.*, *42*(7), 1479–1491.

Bossard, P., and H. Ambühl (1984), Chemismus und Lebewesen im See, in *Der Vierwaldstättersee und die Seen der Zentralschweiz*, pp. 79–100, Keller, Luzern, Switzerland.

Bossard, P., and H. R. Bürgi (2007), Chemische und biologische Prozesse, in *Vierwaldstättersee - Lebensraum für Pflanzen, Tiere und Menschen*,

edited by P. Stadelmann, pp. 122–137, Brunner Verlag, Kriens, Switzerland.

Bossard, P., S. Gammeter, C. Lehmann, F. Schanz, R. Bachofen, H. R. Bürgi, D. Steiner, and U. Zimmermann (2001), Limnological description of the Lakes Zurich, Lucerne, and Cadagno, *Aquat. Sci.*, *63*(3), 225–249, doi:10.1007/pl00001353.

Bührer, H., and H. Ambühl (2001), Lake Lucerne, Switzerland, a long term study of 1961–1992, *Aquat. Sci.*, *63*(4), 432–456, doi:10.1007/s00027-001-8043-8.

Bürgi, H. R. (1987), Long-term development of blue-green-algae in Lake Lucerne with special reference to Oscillatoria (Planktothrix) Rubescens, *Schweiz. Z. Hydrol. Swiss J. Hydrol.*, *49*(3), 375–377, doi:10.1007/bf02538298.

Bürgi, H. R., and P. Bossard (2007), Kleinorganismen in Gewässern, in *Vierwaldstättersee - Lebensraum für Pflanzen, Tiere und Menschen*, edited by P. Stadelmann, pp. 139–159, Brunner Verlag, Kriens, Switzerland.

Bürgi, H. R., and P. Stadelmann (2002), Alteration of phytoplankton structure in Lake Lucerne due to trophic conditions, *Aquat. Ecosyst. Health Manage.*, *5*(1), 45–59.

Bürgi, H. R., P. Weber, and H. Bachmann (1986), Seasonal variations in the trophic structure of phytoplankton and zooplankton communities in lakes in different trophic states, *Schweiz. Z. Hydrol.*, *47*(2), 197–224.

Bürgi, H. R., C. Heller, S. Gaebel, N. Mookerji, and J. V. Ward (1999), Strength of coupling between phyto- and zooplankton in Lake Lucerne (Switzerland) during phosphorus abatement subsequent to a weak eutrophication, *J. Plankton Res.*, *21*(3), 485–507, doi:10.1093/plankt/21.3.485.

Deutschen Einheitsverfahren (DEV) (1972–1989), *Deutsche Einheitsverfahren zur Wasser-Abwasser und Schlammuntersuchung*, VCH, Weinheim, Germany.

Dillon, P. J., and F. H. Rigler (1974), Test of a simple nutrient budget model predicting phosphorus concentration in lake water, *J. Fish. Res. Board Can.*, *31*(11), 1771–1778.

Dokulil, M. (1987), Long-term occurrence of blue-green-algae in Mondsee during eutrophication and after nutrient reduction, with special reference to Oscillatoria-Rubescenst, *Schweiz. Z. Hydrol. Swiss J. Hydrol.*, *49*(3), 378–378.

Dubois, J. P., C. Gillet, N. Hilgert, and G. Balvay (2008), The impact of trophic changes over 45 years on the Eurasian perch, Perca fluviatilis, population of Lake Geneva, *Aquat. Living Resour.*, *21*(4), 401–410, doi:10.1051/alr:2008051.

Duenas, J. F., J. R. Alonso, A. F. Rey, and A. S. Ferrer (2003), Characterisation of phosphorous forms in wastewater treatment plants, *J. Hazard. Mater.*, *97*(1-3), 193–205, doi:10.1016/s0304-3894(02)00260-1.

Eppley, R. W. (1972), Temperature and phytoplankton growth in sea, *Fish. Bull.*, *70*(4), 1063–1085.

Eppley, R. W., and P. R. Sloan (1966), Growth rates of marine phytoplankton - correlation with light absorption by cell chlorophyll alpha, *Physiol. Plantarum*, *19*(1), 47–59, doi:10.1111/j.1399-3054.1966.tb09073.x.

Finger, D. (2006), Effects of hydropower operation and oligotrophication on internal processes in Lake Brienz, PhD thesis, 194 pp., ETH Zurich, Zurich, Switzerland. [Available at http://fingerd.jimdo.com/.].

Finger, D., M. Schmid, and A. Wüest (2007a), Comparing effects of oligotrophication and upstream hydropower dams on plankton and productivity in perialpine lakes, *Water Resour. Res.*, *43*, W12404, doi:10.1029/2007WR005868.

Finger, D., P. Bossard, M. Schmid, L. Jaun, B. Müller, D. Steiner, E. Schaffer, M. Zeh, and A. Wüest (2007b), Effects of alpine hydropower operations on primary production in a downstream lake, *Aquat. Sci.*, *69*(2), 240–256, doi:10.1007/s00027-007-0873-6.

Gächter, R., and A. Marès (1979), Comments to the acidification and bubbling method for determining phytoplankton production, *Oikos*, *33*(1), 69–73.

Gächter, R., A. Mares, and M. M. Tilzer (1984), Determination of phytoplankton production by the radiocarbon method—A comparison between the acidification and bubbling method (ABM) and the filtration technique, *J. Plankton Res.*, *6*(2), 359–364, doi:10.1093/plankt/6.2.359.

Goldman, C. R. (1988), Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California Nevada, *Limnol. Oceanogr.*, *33*(6), 1321–1333.

Goldman, C. R. (1990), The importance of long term limnological research with emphasis on Lake Tahoe and Castle Lake, *Mem. dell'Istituto Ital. Idrobiol. Dott Marco Marchi*, *47*, 221–231.

Goldman, C. R., A. Jassby, and T. Powell (1989), Interannual fluctuations in primary production—Meteorological forcing at 2 subalpine lakes, *Limnol. Oceanogr.*, *34*(2), 310–323.

Golterman, H. L., R. S. Clymo, and M. Ohnstad (1978), *Methods for Physical and Chemical Analysis of Freshwaters*, 213 pp., Blackwell Sci., Oxford, U. K.

Hessen, D. O., P. J. Faerovig, and T. Andersen (2002), Light, nutrients, and P:C ratios in algae: Grazer performance related to food quality and quantity, *Ecology*, *83*(7), 1886–1898, doi:10.2307/3071772.

Jassby, A. D., and T. Platt (1976), Mathematical formulation of relationship between photosynthesis and light for phytoplankton, *Limnol. Oceanogr.*, *21*(4), 540–547.

Jassby, A. D., T. M. Powell, and C. R. Goldman (1990), Interannual fluctuations in primary production - direct physical effects and the trophic cascade at Castle Lake, California, *Limnol. Oceanogr.*, *35*(5), 1021–1038.

Jassby, A. D., C. R. Goldman, J. E. Reuter, and R. C. Richards (1999), Origins and scale dependence of temporal variability in the transparency of Lake Tahoe, California-Nevada, *Limnol. Oceanogr.*, *44*(2), 282–294.

Jaun, L., D. Finger, M. Zeh, M. Schurter, and A. Wüest (2007), Effects of upstream hydropower operation and oligotrophication on the light regime of a turbid peri-alpine lake, *Aquat. Sci.*, *69*(2), 212–226, doi:10.1007/s00027-007-0876-3.

Jeppesen, E., et al. (2005), Lake responses to reduced nutrient loading—An analysis of contemporary long-term data from 35 case studies, *Freshwater Biol.*, *50*(10), 1747–1771, doi:10.1111/j.1365-2427.2005. 01415.x.

Larson, G. L., R. Collier, and M. W. Buktenica (2007), Long-term limnological research and monitoring at Crater Lake, Oregon, *Hydrobiologia*, *574*, 1–11, doi:10.1007/s10750-006-0342-6.

Mazumder, A., and J. A. Edmundson (2002), Impact of fertilization and stocking on trophic interactions and growth of juvenile sockeye salmon (Oncorhynchus nerka), *Can. J. Fish. Aquat. Sci.*, *59*(8), 1361–1373, doi:10.1139/f02–111.

Nielsen, E. S. (1980), Citation classic—The use of radioactive carbon (C-14) for measuring organic production in the Sea, *Curr. Contents/Agric. Biol. Environ. Sci.*, *17*, 12–12.

Platt, T., and A. D. Jassby (1976), Relationship between photosynthesis and light for natural assemblages of coastal marine-phytoplankton, *J. Phycol.*, *12*(4), 421–430, doi:10.1111/j.0022-3646.1976.00421.x.

Platt, T., C. L. Gallegos, and W. G. Harrison (1980), Photoinhibition of photosynthesis in natural assemblages of marine-phytoplankton, *J. Mar. Res.*, *38*(4), 687–701.

Rellstab, C. (2008), Life at low food—Population dynamics and genetic structure of Daphnia in ultra-oligotrophic Lake Brienz, PhD thesis, ETH Zurich, Zurich, Switzerland.

Rellstab, C., V. Maurer, M. Zeh, H. R. Burgi, and P. Spaak (2007), Temporary collapse of the Daphnia population in turbid and ultra-oligotrophic Lake Brienz, *Aquat. Sci.*, *69*(2), 257–270, doi:10.1007/s00027-007-0872-7.

Rodhe, W. (1958), The primary production in lakes: Some results and restrictions of the 14C methods, *J. Cons. Perm. Int. Explor.*, *144*, 122–128.

Sakamoto, M., et al. (1984), Joint field experiments for comparisons of measuring methods of phytosynthetic production, *J. Plankton Res.*, *6*(2), 365–383, doi:10.1093/plankt/6.2.365.

Schlatter, J. W., A. Wüest, and D. M. Imboden (1997), Hypolimnetic density currents traced by sulphur hexafluoride (SF6), *Aquat. Sci.*, *59*(3), 225–242, doi:10.1007/s000270050010.

Sommer, U., Z. M. Gliwicz, W. Lampert, and A. Duncan (1986), The PEG-model of seasonal succession of planktonic events in fresh waters, *Arch. Hydrobiol.*, *106*(4), 433–471.

Steemann Nielsen, E. (1952), The use of radioactive carbon (C-14) for measuring organic production in the Sea, *J. Cons. Perm. Int. Explor.*, *18*, 117–140.

Stockner, J. G., E. Rydin, and P. Hyenstrand (2000), Cultural oligotrophication: causes and consequences for fisheries resources, *Fisheries*, *25*(5), 7–14.

Vallentyne, J. R. (1973), The algal bowl—A Faustian view of eutrophication, *Fed. Proc.*, *32*(7), 1754–1757.

Van Donk, E., D. O. Hessen, A. M. Verschoor, and R. D. Gulati (2008), Re-oligotrophication by phosphorus reduction and effects on seston quality in lakes, *Limnologica*, *38*(3-4), 189–202, doi:10.1016/j.limno.2008.05.005.

Vollenweider, R. A. (1968), Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication, OECD Rep. DAS/CSI/68.27, Organ. for Econ. Coop. and Dev., Paris.

Williams, R. B., and M. B. Murdoch (1966), Phytoplankton production and chlorophyll concentration in Beaufort channel, North Carolina, *Limnol. Oceanogr.*, *11*(1), 73–82.